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Ecological complexity effects on thermal signature of different Madeira island ecosystems.
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Ecological complexity effects on thermal signature of different Madeira island ecosystems.

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Highlights

- Evolution selects ecological complexity that maximize entropy production.
- Higher entropy production levels leads to more attenuated lower temperatures.
- Ecosystem temperature was measured in Madeira island using remote sensing.
- Findings reveal types of ecosystem complexity have different thermal signature.
- Ecosystem disturbance have different thermal impact depending if it's natural or artificial.

Abstract

From a systemic perspective, evolution and natural succession promote the creation of efficient biological structures and processes that capture and dissipate the solar energy, maximizing the entropy production. This ecological complexification results in better ecosystem thermodynamic performance indicated by lower temperature.

In a brief period of evolutionary time human-induced disturbance has altered profoundly the structure and functioning of the Earth System, i.e. ecological simplification.

The objective is to understand whether remote sensing data can be considered appropriate proxy indicators to test if more mature and complex ecosystems have higher entropy production rates which lead to lower and attenuated ecosystem temperatures.

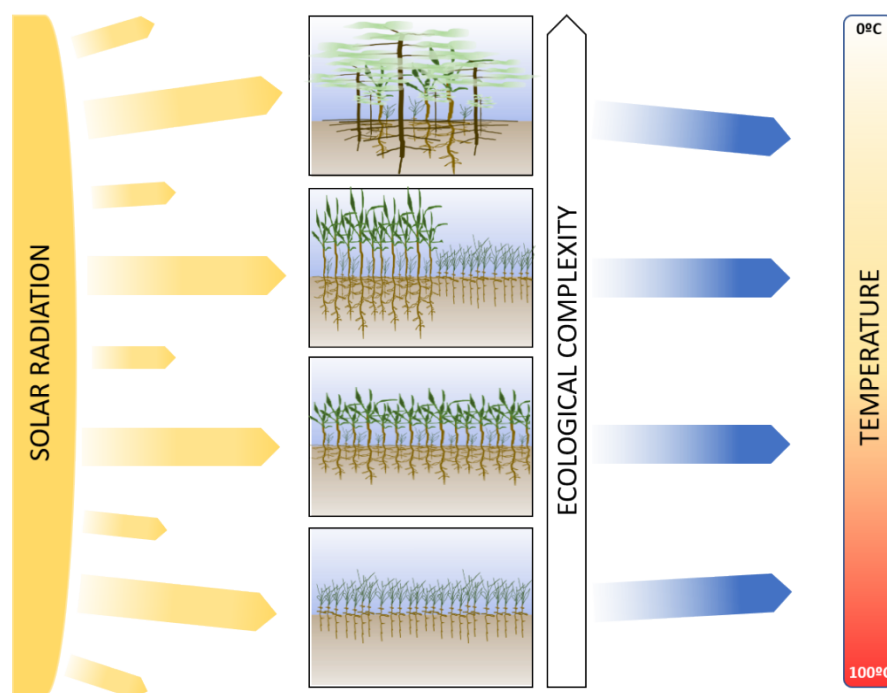
Simple remote sensing measurements of Madeira Island for Thermal Infrared Radiation and Normalized Difference Vegetation Index were used to analyse the surface temperature and biomass cover of Madeira ecosystems spectrum of different states of human-induced disturbance.

The findings revealed it was possible to distinguish between ecosystem types using thermodynamic indicators, where older ecosystems with more complex structures exhibit more attenuated lower average temperatures.

It was also found that habitat heterogeneity can represent either artificial (human) or natural disturbance with opposite consequences in the ecosystem thermal signature, i.e. lower temperature when natural disturbance and higher if anthropogenic disturbance.

Simple thermal remote sensing data can be used as systemic indicator of ecosystem health by reflecting it levels of eco-exergy, i.e the available work energy in the ecosystem.

Graphical abstract



Keywords

Ecosystem health indicator; Eco-exergy; Thermodynamic; Disturbance; Remote sensing; Temperature;

1. Introduction

1.1. Anthropocene influence on Earth eco-exergy

Over the relatively short span of human history on Earth, major innovations, such as the domestication of livestock, adoption of an agricultural lifestyle, and the Industrial Revolution, have triggered baseline shifts in many aspects of the Earth's ecology across all scales, including its thermodynamic character (Lewis and Maslin, 2015), which have contributed significantly to a net global decrease in terrestrial exergy over the last few decades (Jiménez-Muñoz et al., 2012). From a physical (or thermodynamic) point of view, exergy is defined as the amount of work a system can perform when it is brought into thermodynamic equilibrium with its environment, so it is considered as a high quality energy. In natural ecosystems, exergy corresponds to the amount of biomass, information and networks invested during growth and development (Fath et al., 2004; Jorgensen and Norsnielsen, 2007; Jørgensen, 2006a).

Studies (see Crutzen, 2006), on particulate matter trapped in air pockets in the polar ice cap suggest that substantial changes in concentrations of atmospheric carbon dioxide and methane may have started in the late eighteenth century. Within the last 200 years a dramatic increase in human population and economic growth has substantially increased the human appropriation of net primary production (Krausmann et al., 2013), which in turn, has reduced the eco-exergy for non-human species and caused declines in species richness (Haberl et al., 2004). Rapid changes to environmental conditions accelerates many biospheric processes including key parameters such as the turnover of biomass in terrestrial ecosystems (Erb et al., 2016). Environmental degradation is also associated with an increase in the total mass of global human-made structures, such as the stock of materials, including buildings, roads, and factories, and which currently amounts to 792×10^9 tons, rivaling the biomass of all plants on land (circa 900×10^9 tons of dry matter) (Krausmann et al., 2017).

Nearly 35% of the world's land surface has been altered and degraded by the conversion of natural ecosystems to agricultural landscapes, and by the rapid expansion of infrastructure and urban areas (Ramankutty and Foley, 1999), leaving only about one fifth of the global land still regarded as "wilderness" (Sanderson et al., 2002). Humans account today for about 36% of the biomass of all mammals, domesticated livestock account for 60% while wild mammals for just 4% (Bar-On et al., 2018).

Complex ecological interactions manifest in human exploitation of natural resources has affected the functioning of the major natural ecosystems across the planet, and in turn, this has altered their thermodynamic character. The ability of ecosystems to store and dissipate energy has been reduced

by the loss of structures, networks and ecological information (gene pools and functional species), which disrupts resilience and can seriously impair a system's ability to escape collapse (Aoki, 2012; Gunderson, 2001). In turn, any reduction of ecosystem function will impact both directly and indirectly on the ability of the ecosystem to provide the necessary services to support human well-being (Galetti, 2017) and to the systems panarchy, i.e. the interplay between change and persistence, between the predictable and unpredictable (Gunderson, 2001).

1.2. Indicators of ecosystem health

Ecosystem health has traditionally been associated with concepts of ecological integrity, capability of self-restoration, biodiversity, and resilience (Michaelian, 2015). Evaluations for ecosystem health normally include indicators such as presence of keystone species; endemic species; species richness and abundance; functional diversity; immigration of exotic species or emigration of native species; vulnerability to disease and temporary stress, such as that produced by insects, drought, flooding, or fire; nutrient content of the soils or the accumulation of wastes or contaminants. So far there is no existing monitoring approach that can sufficiently assess and predict vegetation health on its own (Lausch et al., 2018a). In most cases, the necessary planning and field-based assessment used to monitor ecosystem health is difficult and expensive and even then may only provide a limited interpretation of conditions (Michaelian, 2015).

Life on Earth rises and evolves predominantly through the thermodynamic imperative of maximizing the dissipation of solar photon flux by increasing its eco-exergy. After the initial capture of energy across a boundary, ecosystem complexity development is possible by an increase of the physical structure (biomass), an increase of energy and matter cycling (network) and an increase of diversity of species and functions (information embodied in the system) (Jørgensen, 2006a). All three growth forms imply that the system is moving away from thermodynamic equilibrium and all three growth forms are associated with an increase of the eco-exergy stored in the ecosystem and the energy through flow in the system (power). When cycling flows increase, the eco-exergy storage capacity, the energy use efficiency and space-time differentiation all increase.

Eco-exergy is a measure of 'quality' or available work energy in an ecosystem (Jørgensen, 2006a) and has been applied successfully in many studies to assess ecosystems health where it has proved to be successful in evaluating the organizational state of wetlands and aquatic ecosystems (Jørgensen, 2002, 1990; Lin et al., 2018; Lu et al., 2011; Romero and Linares, 2014). Evolution and natural succession promotes the creation of biological structures and processes that capture and dissipate the solar energy, accompanied by the emergence of entropy according to the Second Law of thermodynamics (Aoki, 2012; Zotin, 1990, 1984). The same principle has also been applied in studies

on forest ecosystems to test for differences in thermodynamic function between old growth and new plantations (Norris et al., 2011; Schneider and Kay, 1994).

The initial work of Lotka (1922) concerning the flow of energy through an ecosystem, promoted a shift in ecosystem analysis from a reductionist paradigm to one more systemic based on physical laws. Later, Schrodinger (1944) pointed out that living systems were under the dictates of thermodynamic law and that biological structure and processes were maintained by a continual inflow of negative entropy, at the expense of an entropy increase to the environment. Prigogine (1965) initially developed the physical and mathematical groundwork for the description of non-equilibrium phenomena, and in later years Zotin (1990), Schneider and Kay (1994), advanced the use of the concept of non-equilibrium thermodynamic to explain living systems on all levels, including ecosystems.

There are several reasons why ecosystems analysis framework should be grounded in non-equilibrium thermodynamic theory (Michaelian, 2005). The most obvious reason is the laws of thermodynamics help us understand the structures and processes in nature across all scales. Thermodynamics provides a unified hierarchical description of nature and the universe, and allows for detailed studies of the macroscopic behaviour of complex systems, benefiting from a reduction in the number of effective variables.

The thermodynamic function of an ecosystem is, in part, explained by the responses of plants to changes in growing conditions including periods of extreme environmental events. Plants will optimize transpiration by removing the heat of the dissipated photons at the leaf surface and converting it into latent heat through a process of evapotranspiration. Together, photon dissipation and transpiration account for much of the free energy dissipation performed by plants and can be measured in the form of microclimatic temperature (Michaelian, 2015, 2012, 2011; Norris et al., 2011). At the landscape level, ecosystems are moved away from thermodynamic equilibrium by growth in physical structure (biomass); an increase of the network (more cycling); and by an increase in diversity invested in the system (Fath et al., 2004; Jørgensen, 2006b; Jørgensen and Fath, 2004; Schick et al., 2019; Schneider and Kay, 1994) but evidence is still missing (Cushman, 2015).

Most of the studies carried out using temperature as an indicator of ecosystem function have been field-based and have not used remote sensing techniques at larger scales. More recently, the availability of satellite thermal imagery has provided opportunities to examine 'ecosystem thermodynamics' (the thermodynamic character of ecosystems), at landscape scale but there are limitations to its effectiveness (Cui et al., 2013; de C. Teixeira et al., 2015; Michaelian, 2015). The temperature measured in an ecosystem is a function of the intensity of the incoming solar radiation

and this can present difficulties when attempting any comparative analysis across space and time because of atmospheric and seasonal variations. Ecosystems do not emit light in a black-body spectrum, which poses a problem when working with the concept of equilibrium temperature (Michaelian, 2015). Notwithstanding, the accuracy, reproducibility, simplicity and ease by which remote sensing can be applied to ecosystem studies justifies its continued use in this field of research. Collaboration of remote sensing experts with the ecosystem user community will be imperative to benefit from novel satellite missions (Pause et al., 2016). Land surface temperature is directly connected to processes of water and energy fluxes in soils and vegetation and is a key attribute in models designed to assess the physical state of the environment (Moran, 2004).

The research question addressed in our paper is whether remote sensing data, in particular measurements for thermal imagery and Normalized Difference Vegetation Index (Gamon et al., 1995; Godinho et al., 2016), can be considered appropriate proxy indicators for eco-exergy in terrestrial ecosystems. The hypothesis tested was as follows, “for a given state of incident photon flux, more mature and complex ecosystems have higher entropy production rates and together with greater energy storage capacity lead to lower and attenuated ecosystem temperatures” (Pierre L. Ibisch et al., 2010; Lin et al., 2018; Michaelian, 2015; Norris et al., 2011; Schneider and Kay, 1994; Ulanowicz and Hannon, 1987).

2. Methods

2.1. Madeira Case Study

Madeira is a Portuguese island covering 740.7 km² and located in the north Atlantic Ocean, within the climatic region classified as Mediterranean. The average annual temperature varies between 8°C at the highest altitude and 19°C in coastal areas (based on 1961–1990 climatic series). On the highest windward slopes of Madeira, annual rainfall exceeds 1,250 mm although much of it falls between the months of October and April.

Madeira has both endemic woods and exotic plantations, namely, *Pinus pinaster* and *Eucalyptus spp*, at middle to higher altitude. At lower altitudes the landscape is a mixture of commercial agriculture (banana plantations and crop lands), and urban development. The native humid forest covers 15,000 hectares and is dominated by *Laurissilva* (see appendix). With 90% remaining as intact primary forest, it is the single largest biotope of its kind in the world and contains 15% of Madeira's endemic species (Capelo et al., 2005). However, over the years it has been subjected to many stresses, including deforestation, fires, introduction of exotic species and climate change (Cruz et al., 2010).

2.2. Satellite imagery processing

Detail data generated from satellite imagery was used to assess and quantify vegetation biomass based on an index for the photosynthetic capacity of plants - the Normalized Difference Vegetation Index (NDVI, Tucker, 1979). To assess surface temperature, remote sensor readings for the top of the atmosphere brightness temperature were used, specifically, Thermal Infrared (TIR) energy emitted by the Earth's surface, the intensity of which is a function of surface temperature (Zanter, 2016). The chosen satellite was the Landsat 8 made available by the USGS EROS Centre, which provides data in the form of calibrated scaled Digital Numbers (DN) representing multispectral image measurements generated by both the Operational Land Imager (OLI) and Thermal Infrared Sensor (TIRS). Thirteen images were selected between August 19th, 2013 and July 8th, 2015 for periods of the day when cloud cover was recorded to be lower than 10% of the total area. The data was downloaded from the USGS EarthExplorer website.

NDVI values were calculated using the Landsat 8 Data handbook (Zanter, 2016) by initially converting digital numbers to reflectance values, using the coefficients provided in the Landsat 8 OLI metadata file in Equation 1. Equation 2 was applied to reflectance values (bands 4 & 5), to correct

194 for the angle of the sun. Equation 3 was used with the bands 4 (RED) and 5 (NIR) to give the final
195 NDVI read-out.

196 *Equation 1* $\rho\lambda' = Mp Q_{cal} + Ap$

197 Where:

198 $\rho\lambda'$ = TOA planetary reflectance, without correction for solar angle.

199 Mp = Band-specific multiplicative rescaling factor from the metadata

200 Ap = Band-specific additive rescaling factor from the metadata

201 Q_{cal} = Quantized and calibrated standard product pixel values (DN)

202 *Equation 2* $\rho\lambda = \rho\lambda' / \sin \theta_{SE}$

203 Where:

204 $\rho\lambda$ = TOA planetary reflectance

205 θ_{SE} = Local sun elevation angle of the scene centre, provided in the metadata (Sun Elevation).

206 *Equation 3* $NDVI = (NIR - RED) / (NIR + RED)$

207

208 The brightness temperature was calculated by transforming the digital numbers into spectral
209 radiance, adding the radiance scaling factors provided in Equation 4 in the metadata file.
210 Temperature values, in Kelvin, were calculated using Equation 5 before converting to degrees
211 Celsius. Clouds were removed using the cloud mask provided by the USGS EROS Centre.

212 *Equation 4* $L_{\lambda} = M_L * Q_{cal} + A_L$

213 Where:

214 L_{λ} = Spectral radiance (W / (m² * sr * μ m))

215 M_L = Radiance multiplicative scaling factor for the band.

216 A_L = Radiance additive scaling factor for the band.

217 Q_{cal} = L1 pixel value in DN

218 *Equation 5* $T = K2 / \ln((K1 / L_{\lambda}) + 1)$

Where:

T = TOA Brightness Temperature, in Kelvin.

K1 = Thermal conversion constant for the band

K2 = Thermal conversion constant for the band

Using altitudinal data provided by the Regional Secretariat for Environment and Natural Resources for Madeira (2017), a digital elevation model with a spatial resolution of ten meters was used to aggregate some of the abiotic conditions into classes, based on altitude slope and aspect. Thirty-six abiotic classes were generated using a combination of the abiotic conditions. Then, for each class, the NDVI and TIR statistics were calculated for areas over one hectare to avoid the influence of edge effect.

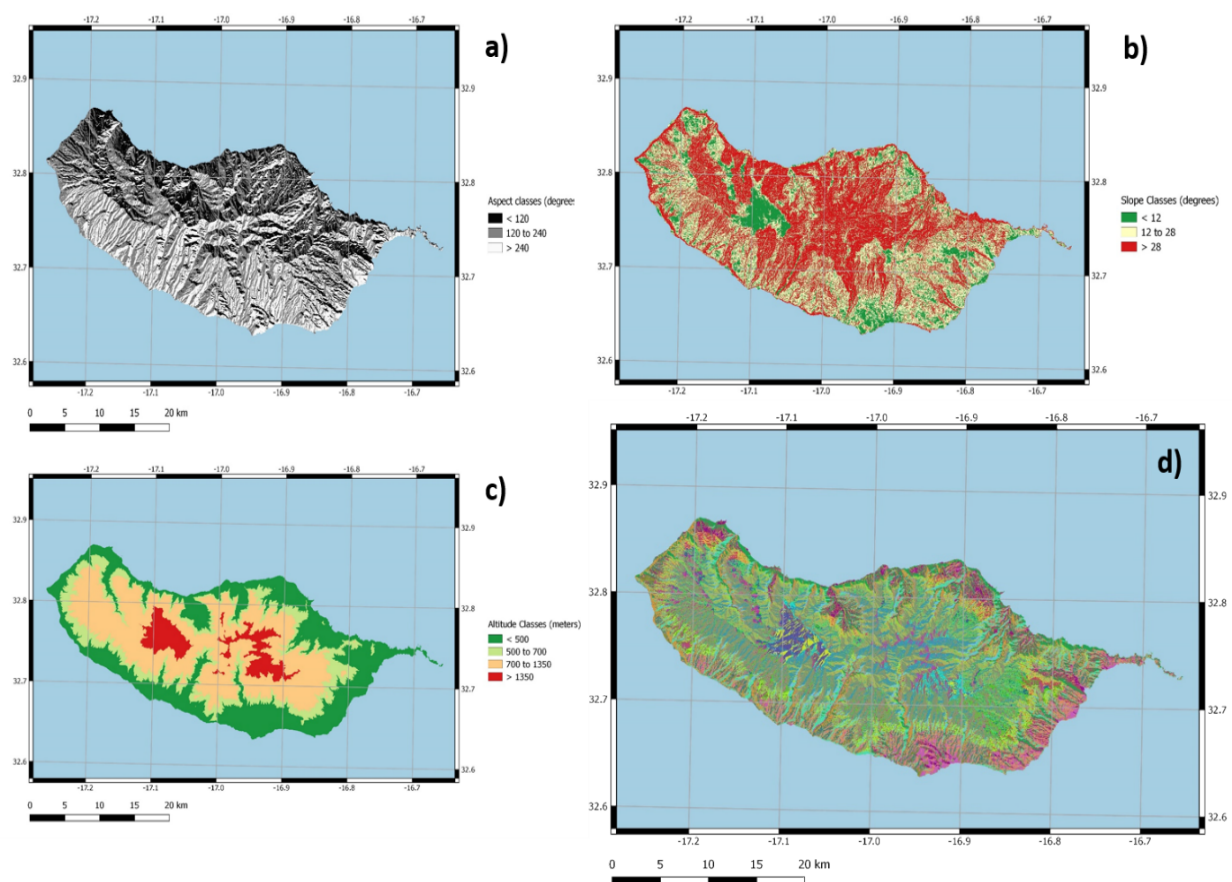


Fig.1 Abiotic homogenization. a) Aspect Classes for the Madeira Island based on a DTM with ten meters resolution; b) Slope Classes for the Madeira Island based on a digital elevation model with ten meters resolution; c) Altitude Classes for the Madeira Island based on a DTM with ten meters resolution; d) Abiotic homogenization by combining slope, altitude and aspect classes, giving a total of 36 new classes

2.3. Statistical analysis

All statistical analyses was carried out using the R programming language (R Core Team, 2016), together with the additional packages - "Hmisc" (Harrell Jr, 2016) and "lme4" (Zeileis and Hothorn, 2002). To increase statistical robustness, data was first cleaned by removing very small data sets, for instance, in cases where abiotic classes were below 4 observations. Then, all classes that exhibited only native or only non-native ecosystems were excluded. Lastly, those ecosystems with three or less observations were also excluded from the final data set.

Linear regressions were tested for Heteroscedasticity using the Breusch-Pagan test, and to test for normal distribution in the model residuals the Shapiro-Wilk Normality Test was used. If these assumptions were violated, spearman correlations were used instead (Fig. 1). For the linear regressions (Fig. 3), a weighted least squares approach was employed, using area size of the polygon as weights. For group wise comparisons (Fig. 2), a Wilcoxon Rank Sum test was used, as data was found to be non-normal using the Shapiro-Wilk Normality Test.

2.3.1. Site conditions standardisation

Before any analysis could be done it was necessary to standardise as best as possible other environmental factors related to topography. To test the effect on temperature of 36 abiotic classes an analysis of deviance (type II tests Wald Chi-square test), based on the linear mixed effects model was used. The results indicated that temperature was likely to be under the influence of other factors rather than any of the 36 abiotic conditions (TIR mean returned the following result, LR Chisq = 180.87, $\text{Pr}(> \text{Chisq}) < 2.2\text{e-}16$). Seasonality was also included in the standardising process. Satellite images were initially grouped according to season and the linear regression slope between biomass and temperature for all abiotic classes was calculated. The results (Fig.2) revealed higher absolute values for both spring and summer seasons, i.e. stronger correlation. Data with the strongest coefficient of determination for linear regression were used during the following steps of the analysis.

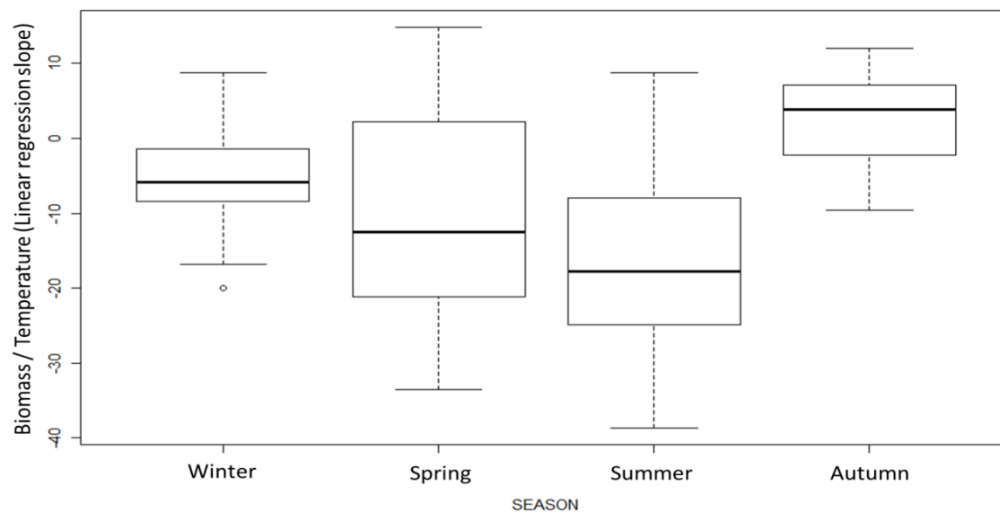


Fig.2 Relation between temperature and biomass for every image and every abiotic class clustered by season. The boxplot midline is the median, with the upper and lower limits of the box being the third and first quartile (75th and 25th percentile) respectively and the whiskers will extend up to 1.5 times the interquartile range from the top (bottom) of the box to the furthest datum within that distance

2.3.2. Research questions tested

To understand whether there is any relation between ecosystem biomass, ecosystem type, habitat heterogeneity and its thermal signature (i.e. temperature), the following parametric and non-parametric correlations were carried out to test for significance.

- There's a relation between ecosystem temperature (TIR mean) or variability (TIR std) and it biomass density (NDVI mean) or biomass variability (NDVI std)? (see [Fig.3](#))
- There's difference in ecosystem temperature (TIR mean) for ecosystems with same biomass density (NDVI mean), but different ecosystems types (Native vs no-native)? (see [Fig.34](#))
- There's difference in ecosystem temperature (TIR mean) or variability (TIR std) for the same ecosystem type but different types of disturbance (habitat heterogeneity – NDVI std)? (see [Fig.5](#) and [Fig.6](#))

3. Results

3.1. Surface biomass and temperature

Irrespective of the type of biomass and abiotic class generated on Madeira ([Fig.1](#)), the results from our study demonstrated a significant drop in both the average temperature (TIR mean values), and also in temperature variability (TIR std values), as the density of vegetation biomass (NDVI mean) increased (

283 Fig.3, circle symbol). Within the general trend, more subtle differences were observed between sites
 284 with different abiotic conditions, and also between the four main biotic types, namely, native forest,
 285 pine and eucalyptus plantations, and banana crops (Fig.4).
 286 Results also revealed a significant positive correlation between temperature and the degree of
 287 variability in biomass cover, both in terms of the average temperature and temperature variability (
 288 Fig.3, triangles symbol)

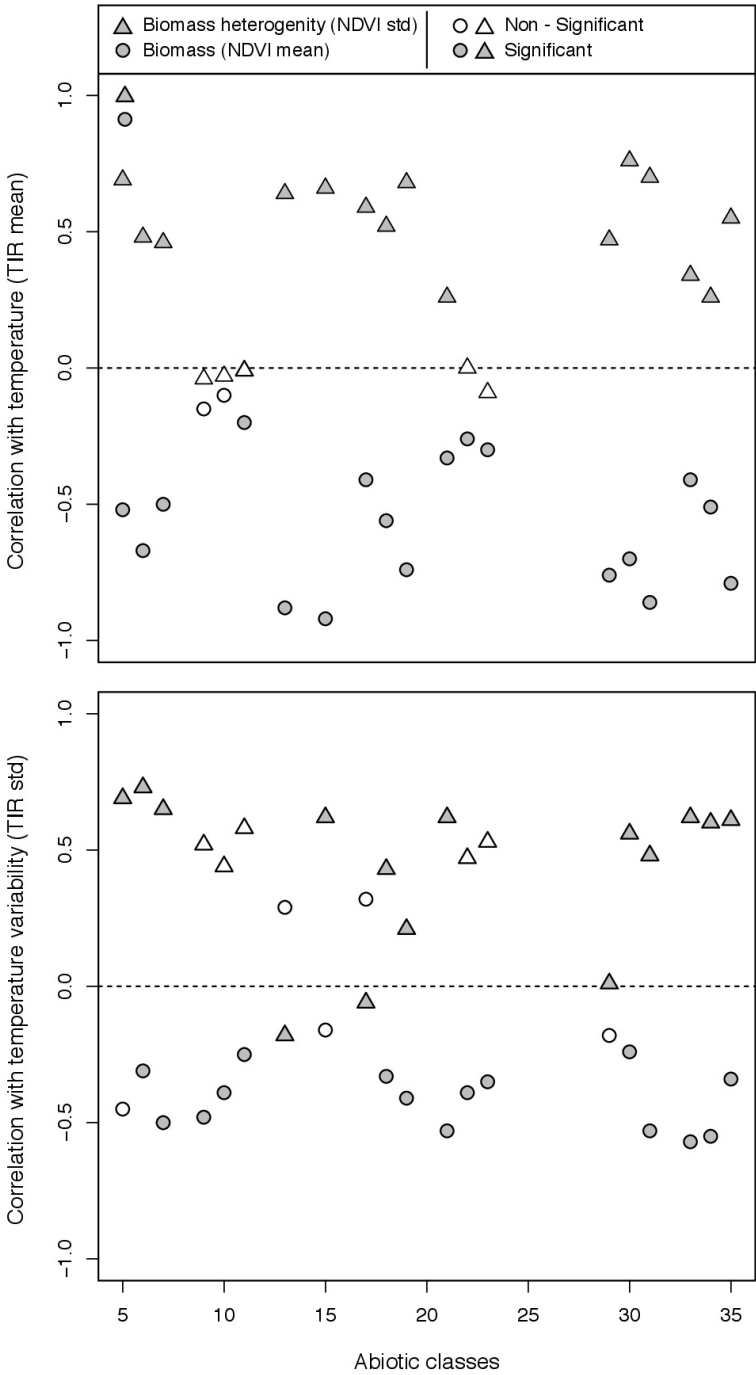


Fig.3 Spearman correlation between biomass (mean-circle and heterogeneity-triangle) and temperature (above mean temperature - TIR mean, below temperature variability - TIR std) for every 36 abiotic class. Data is shown only if there were a minimum of 5 total areas, at least 3 areas per group and both native and non-native ecosystems in each abiotic class. Open symbols depict non-significant correlations; filled symbols depict significant correlations ($p < 0.05$)

3.2. Ecosystem types and temperature.

When assessing temperature readings for different land cover types with similar abiotic conditions and comparable surface biomass (NDVI values), the natural forests appear to reduce significantly both the average daily temperature and the degree of fluctuation in contrast to the younger, non-native plantations. Fig.4 shows that of 47 total comparisons, 36 of them (77%) are significantly different in temperature, suggesting a link between the type of ecosystem and local temperature conditions. Furthermore, landscapes dominated by native vegetation have lower temperature in 100% of all classes if just considering the results that are statistically significant (89% if considering all the classes that are compared).

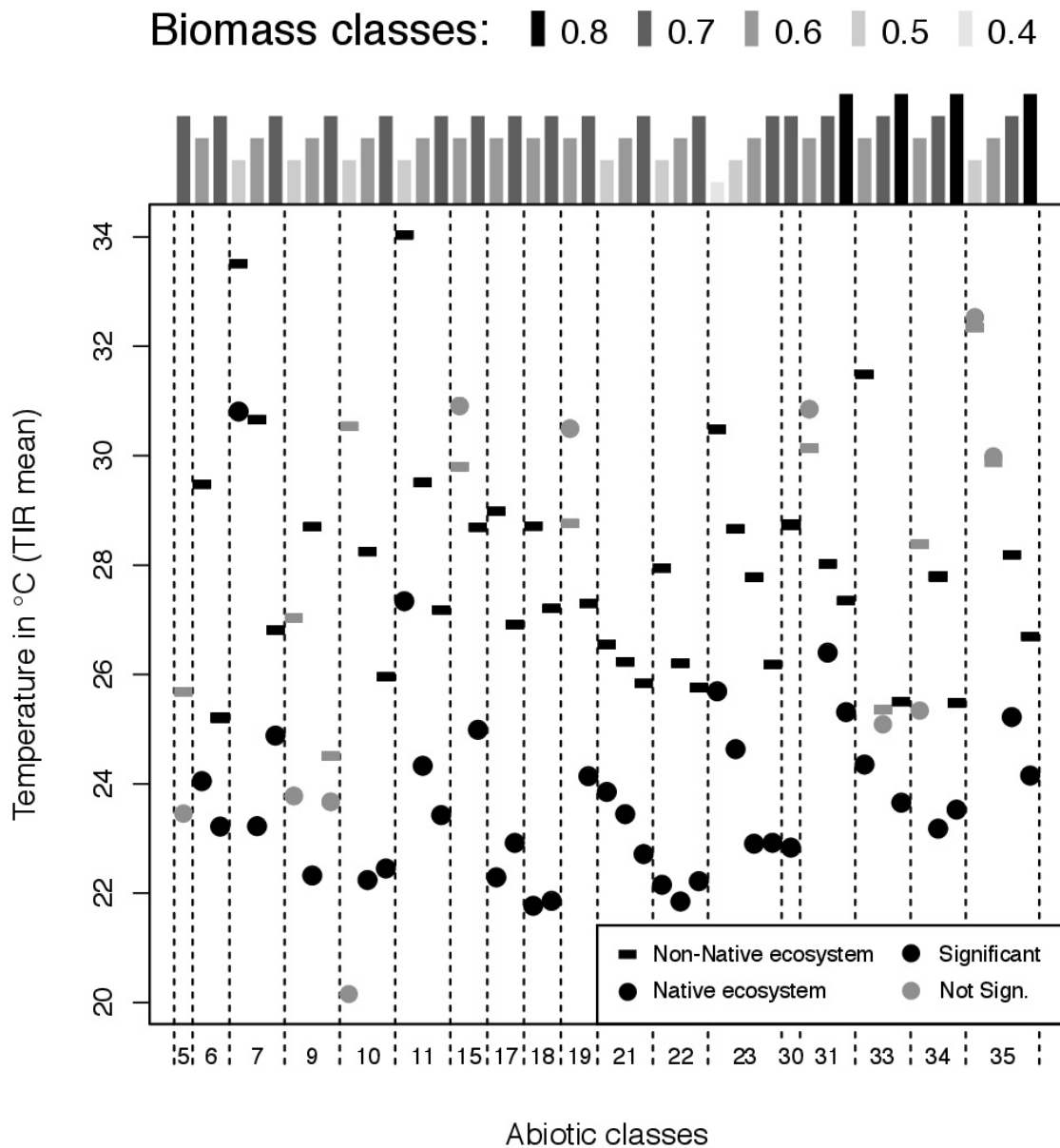


Fig.4 Relation between type of ecosystem (native vs non-native) and temperature for areas with the same biomass class within the abiotic class. Significance was assumed at $p < 0.05$

3.3. Habitat heterogeneity and temperature

A comparative analysis between the different land cover types using data for temperature and habitat heterogeneity (a proxy of species richness and biomass patchiness (Gould, 2000)), reveals a significant negative correlation between average temperatures and habitat heterogeneity in native forests, , while the trend is opposite for both no-native species plantations (Figure 5).

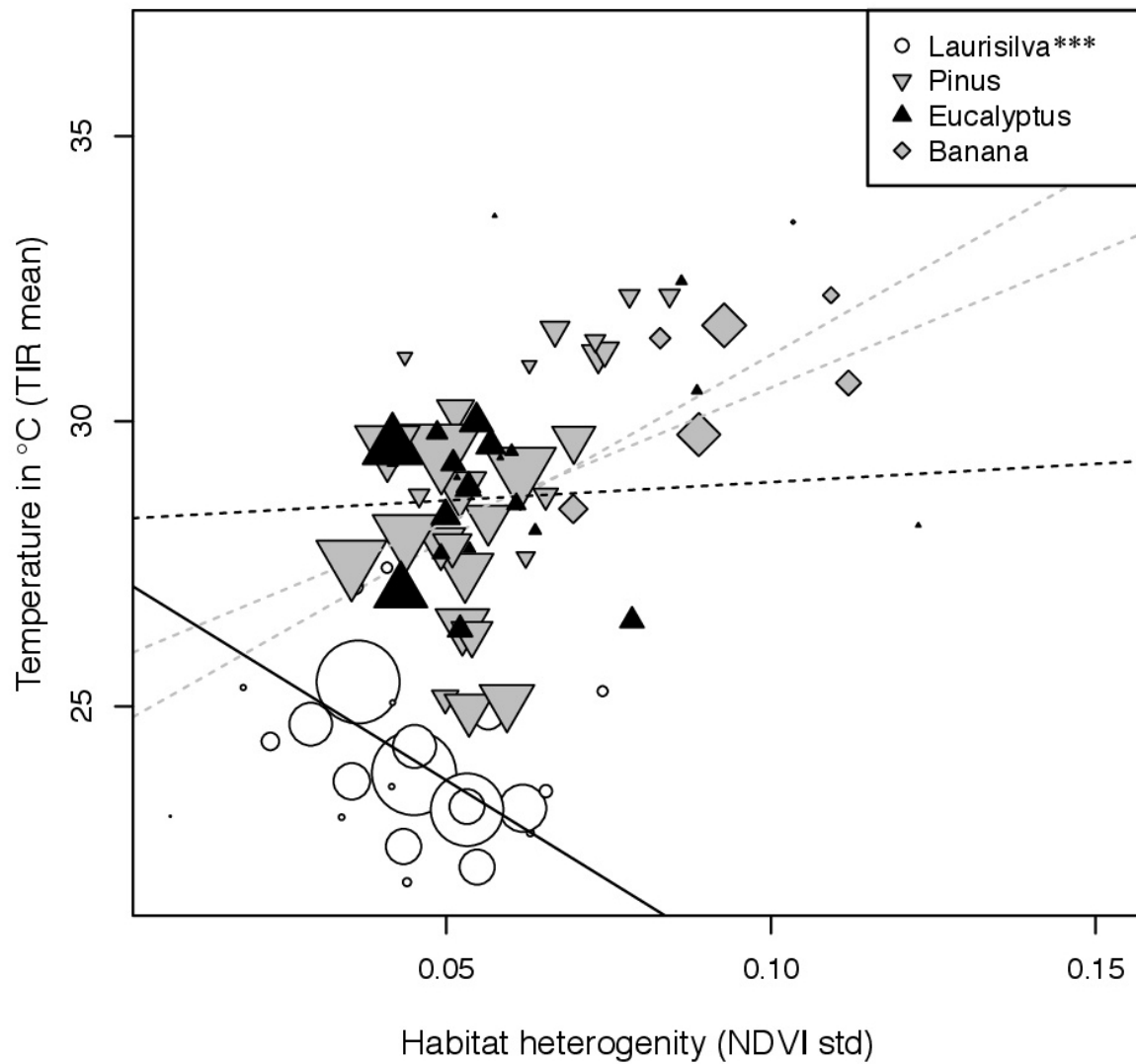


Fig.5 Relation between habitat heterogeneity (NDVI std) and temperature (TIR mean) for four different types of ecosystems: Native (Laurisilva) and non-native (Pine forest, Eucalyptus forest and Banana plantation). Symbol size relates with area size. Continuous lines indicate significant linear regressions (Asterisks depict p-values * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$) dashed lines represent non-significant regressions

When relating the habitat heterogeneity with temperature variability in non-native forests (*Pinus* and *Eucalyptus*), a significant positive correlation is revealed (Fig.6). But in the case of native laurissilva forests and banana plantations there is no significant difference although the overall temperature variation is lower in both these two ecosystems.

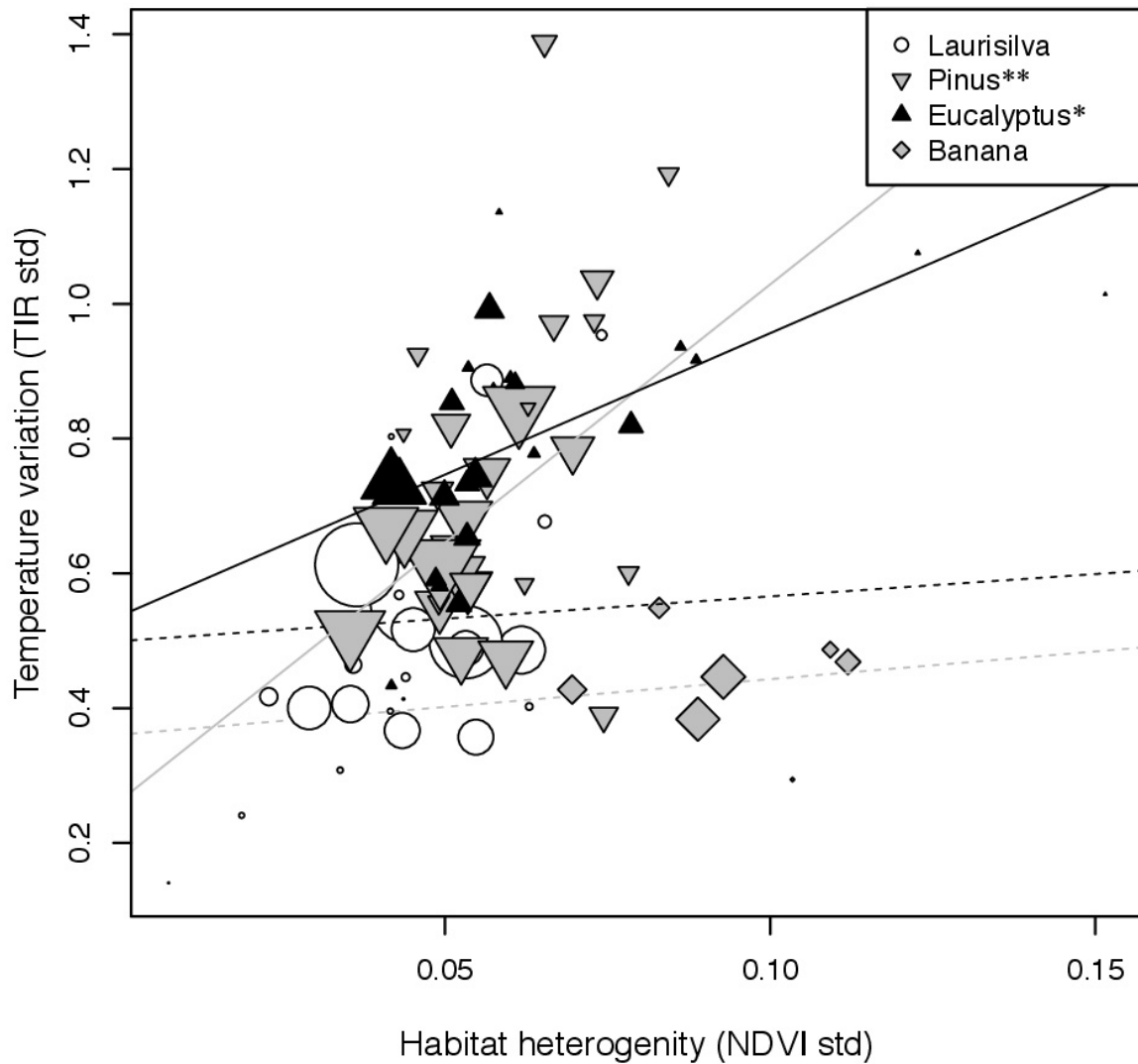


Fig.6 Relation between habitat heterogeneity (NDVI std) and temperature variability (TIR mean) for four different types of ecosystems: Native (Laurissilva) and non-native (Pine forest, Eucalyptus forest and Banana plantation). Symbol size relates with area size. . Continuous lines indicate significant linear regressions (Asterisks depict p -values * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$) dashed lines represent non-significant regressions

4. Discussion

4.1. Spatial and temporal patterns

The use of temperature as an ecosystem health indicator when comparing different land cover types over time is complicated by a number of factors linked to both spatial and temporal scales of resolution (Michaelian, 2015). For example, satellite thermal imagery readings are a function of the intensity of incoming solar radiation and limitations are set by the spatial variability of a habitat such as its altitude, slope and aspect. Also, these spatial variables better explain differences in native vegetation cover than societal variables like human population density (Norder et al., 2020). In this study the problem was partly solved by comparing sites with near to identical or very similar topographical relief – a process of standardising physical site conditions.

Our analysis of the temporal patterns (*Fig.2*) confirmed seasonal variations and suggest that when there is greater solar energy input and there's no abiotic limitation (ex.: soil moisture), the ecosystem responds with a stronger capacity to integrate and dissipate incoming energy, thus, increasing the export of entropy, as stated in theory (Aoki, 2012; Fath et al., 2004; Jorgensen and Norsnielsen, 2007; Jørgensen, 2002), and as revealed in field trial experiments (Michaelian, 2015; Norris et al., 2011). One could expect a better performance during spring when compared with the summer due to higher levels of precipitation but in Madeira Island this was not the case because of the unusually high levels of rainfall that also occur during the summer season. The summer precipitation average is between 50mm and 150mm (Borges et al., 2008; Gomes et al., 2015).

4.2. Eco-exergy and Temperature

The landscape of Madeira is dominated by natural forest vegetation (Laurissilva) on slopes and high ground; mixed non-native tree plantations in similar terrain and lowlands; and agricultural crops, in particular banana across the fertile lowlands and plains. The native Laurissilva forest has retained remnants of old growth stands dating back to 5 to 6 million yrs (Capelo et al., 2005). This native forest ecosystem is rich in species diversity and supports a high number of endemic species as well as a largely undisturbed complex trophic structure. The level of biomass, networks and information invested in the ancient forest is believed to contribute to the complex nature of ecosystem function, which in turn, promotes higher levels of 'eco-exergy' in the system than is to be found in degraded and simplified ecosystems such as crops and silvicultural plantations.

The evidence revealed in our study for a relationship between biomass and thermal radiation supports the findings of previous smaller scaled site-based experiments that identify obvious incremental temperature attenuation and decreases in mean daily temperatures as biomass

increases. Also, the results from the remote sensing analysis that show a negative correlation between biomass and average temperature (

Fig.3) is supported by different field-based studies (Michaelian, 2015; Norris et al., 2011; Schneider and Kay, 1994; Wagendorp et al., 2006).

Variations in biomass and corresponding changes in temperature are quite likely to relate to the ecosystem's thermodynamic mass. However, biomass is not the sole factor responsible for variation in local temperature. The native ecosystem, *Laurissilva*, recorded significantly lower temperature readings, even in areas where biomass appeared to be similar to stands of non-native forest – eucalyptus and pine. The implication is thermodynamic function in ecosystems is attributed to more than just the biomass, and is possibly influenced by the intricate networks and information inherent in the biomass, in other words, the biodiversity and connectivity embedded in the ecosystem biomass (see Fath et al., 2004; Jørgensen, 2002). As an ecosystem grows and matures over time energy pathways become more sophisticated and efficient (Jorgensen and Norsnielsen, 2007).

The native forest on Madeira has evolved over 27 million years (Fernández-Palacios, 2011), time enough for the ecosystem to develop ecological complexity, in other words, more local interactions between individual components, feedbacks between processes occurring at different scales, amplification of minor variations in initial conditions and the emergence of new properties. As is the case with most old growth forest, growth of a mature, long-term established ecosystem is at an optimum state of function in terms of biomass, information and networks and this is reflected in the capacity of the system to store and dissipate incoming energy and to provide a more thermodynamically stabilized functional condition (Jørgensen, 2006b). Many key ecological attributes, including dead wood and wood density, are fundamental to the thermodynamic function of an ecosystem (see Schick et al., 2019; Pandapotan Situmorang et al., 2016). The ability of mature and diverse ecosystems to generate higher levels of stored and usable energy (eco-exergy), influences heat storage and exchange, due to a more efficient use of solar energy and entropy production maximization, leading to lower and attenuated ecosystem temperatures when compared with cultural ecosystems that are less biodiverse, with less soil organic matter and have higher disturbance.

4.3. Habitat heterogeneity, adaptive cycle and temperature

Mesoscale landscape heterogeneity is often expressed as a mosaic of habitat types that correspond to variations in substrate, moisture levels and disturbance. The biomass (NDVI) variability level can be used as a proxy for species richness and patchiness in biomass cover, i.e. the heterogeneity of a habitat (Gould, 2000). In previous studies ecosystem heterogeneity has been used as a proxy

indicator for its information and networks (Fath et al., 2004). Our results (*Fig.5*) indicate lower temperature (TIR) readings in parts of the landscape where there is similar recorded biomass values but greater heterogeneity in the native forest ecosystem. The assumption made is natural disturbance contributes to structural complexity and essential emergent properties for effective ecosystem growth and function, a view shared by Gould (2000). The pattern is very different for ecosystems that have been altered and shaped by human-induced disturbance. In the non-native ecosystems regular management intervention causes changes in levels of biomass, for example, the extraction of large, mature trees and the removal of dead wood. Changes to patch dynamics, patch shape and configuration as a result of harvesting, thinning and establishment operations, and at a finer scale, alterations to soil conditions and local hydrology have caused widespread disruption to ecosystem structure and function and this is reflected in higher temperature (TIR) values for these habitats.

Quantitative estimation of the health of ecosystems affected by anthropogenic stressing is one of the most challenging problems to environmental state monitoring (Gornyy et al., 2010). In this study, the effects of heterogeneity on the thermodynamic function of an ecosystem in contrasting native forest under natural dynamics and intensively managed non-native plantations are portrayed as being diametrically opposed. Induced disturbance appears to break down the structures and networks necessary to dissipate and store energy in a system (Gunderson, 2001). Natural disturbance at certain scales of resolution allow for the systems to retain vital environmental legacies in the form of networks, biomass and information, and this aids recovery (Sundstrom and Allen, 2019). Anthropogenic disturbance is very different in character at many levels, and appears to break down or disrupt these structures, thus reducing functional diversity and redundancy, and possibly shifting the ecosystem towards a more simplified ecological regime (Wagendorp et al., 2006).

The different influences of ecological heterogeneity on the thermodynamic function of an ecosystem (see *Fig.5*), can be explained using concepts of natural succession and the adaptive cycle (Gunderson, 2001; Holling, 1985; Sundstrom and Allen, 2019). Natural heterogeneity is represented by three slightly different but related phases. One of the phases is post disturbance recovery, for example after a severe storm and landslide as was represented by the early succession stages of growth in the native laurissilva forest. In these disturbed stands remnant legacies from the last successional phase, a 'seeding' environment with both living and dead biomass, are apparent, and play an important part in the recovery of a system by providing much needed resources for building new structures, networks and generating new biomass order. They also provide some microclimatic resilience under conditions of change. The last phase is the mature, or pre-collapse phase, where

maximum biomass, network and information emerge with the establishment of efficient energy pathways, where photon dissipation is maximised, i.e. entropy production maximization. The development of networks and information is contingent on time and natural processes. In the case of non-native forests and other modified landscapes both time and natural processes are significantly altered (frequency of cutting and plantation) and shaped (simplified) to the extent that thermodynamic function is impaired. Without the legacies in the post-disturbance phase or the biomass and information banks in the over-store phase, modified and managed ecosystems have effectively had their cycles shortened or tightened, in other words, unlike native forests, they are operating without inbuilt time lags and buffers.

Ultimately, the thermodynamic mass and functional capacity of a system is altered by human disturbance and if radical measures are not taken to mitigate the impacts of human intervention ecosystems will degrade and lose the capacity to provide essential services such as temperature amelioration. An ecosystem-based approach to the management of cultivated landscapes (see Jørgensen, 2006b), that includes an assessment of ecological function, specifically, ecosystem thermodynamic function, is essential to the development of environmentally sustainable land use practice.

5. Conclusion

This study corroborates earlier research findings on ecosystem thermodynamic function in mixed landscapes (see Lu et al., 2011; Norris et al., 2011), but it has also brought fresh insights in to rapid techniques and suitable indicators for assessing ecosystem growth factors in large landscapes. However, there will always be the problem of 'lost resolution' during the process of scaling up from the experimental plot to the larger landscape (Michaelian, 2011). For instance, whether the use of NDVI in satellite imagery is subtle enough to provide an accurate comparison of living biomass across ecosystems. Ideally, any large scale assessment of ecosystem thermodynamics of the kind carried out in Madeira would be coupled with an in-field, plot-scaled analysis of biomass density and microclimatic temperature (see Norris et al., 2011). In our case, the findings have been interpreted in the wider context of similar research (see Freudenberger et al., 2012; Lausch et al., 2018a; Norris et al., 2011).

Notwithstanding, the results of our study conform to both the conceptual model for ecosystem thermodynamics and complex systems offered by Jørgensen et al. (2007), and also align with earlier field plot studies. That is to say, older, more mature native ecosystems (in our case the Laurissilva

forests), appear to be more efficient at storing and dissipating incoming energy. Theory about ecosystem complexity argues for the importance of biomass, information and networks in providing effective ecosystem function, and in the field, the proxy indicator for forest biomass is typically recorded as above ground biomass and volume of woody matter. An increase in above ground biomass has produced lower microclimatic ambient and surface temperatures, and also greater temperature attenuation. The rather cruder measure of biomass – NDVI, used in our study, has mimicked the findings of previous field-based studies which suggests there is potential for using it in the assessment of ecosystem function at landscape scale.

The more subtle assessment of ecosystem networks and information in the context of ecosystem thermodynamics is not covered so much in the literature. The study by Norris et al (2011), proposed the use of plant trait indices and plant species richness as indicators of information and networks. Similarly, work by Freudenberger et al. (2012), used species and functional richness to assess ecosystem function in large landscapes. For our study we applied a rather more inductive approach by ‘smoothing’ or standardising data for abiotic and biomass in comparable classes, before comparing old native stands with young non-native plantations. While our results lead us to conclude that there are other factors apart from biomass that contribute to ecosystem thermodynamic function, there is no specific predictive set of indicators identified or tested for in the analysis. We would have to conclude that ecosystems are so complex that at the end of the day we have to accept the prevalence of unknowns in nature, and fall back on simple but robust theories of physics, in this case, thermodynamics.

The argument for simple but robust and rapid methods of assessing ecosystems is all the more relevant and compelling in the current climate of environmental uncertainty and change. If techniques such as those used in this study, generate trends and patterns recognisable within a wider cluster of similar studies, they should be acceptable sources of evidence for informing management. Rather than get lost in a Cartesian spiral of atomistic analysis it seems more appropriate to adopt a post-normal science perspective of accepting the unknowns of ecosystem complexity by adjusting the analysis and interpretation of experimental investigation to simple but fundamental laws of physics (P.L. Ibisch et al., 2010). The next step is to translate the findings in to the language of practitioners. Forest managers, decision makers, and politicians need to be able to make rapid decisions that are evident-based (Lausch et al., 2018b).

Our findings show that more simple and human disturbed ecosystems have higher temperatures when compared with natural ecosystems with the same abiotic conditions and even the same surface biomass. Temperature indicates the ecosystems thermodynamic performance, where

489 healthy ecosystems have greater thermodynamic mass, corresponding to higher levels of
490 complexity, longer adaptive cycles, stronger legacy, higher buffer capacity, as well as lower and
491 more attenuated temperature. In contrast, human-disturbed or modified ecosystems have higher
492 and erratic temperature indicating a state of “fever”.

493 The thermodynamic mass and ecosystem exergy of global ecosystems has been affected by
494 anthropogenic disturbance in its many forms. Climate change is both a direct and indirect result of
495 human disturbance, including the loss of ecosystem biomass; land use change and ecosystem
496 simplification; loss of landscape and habitat connectivity; and the loss of biodiversity with all the
497 necessary information and networks necessary for ecosystem function. This loss of ecosystem self-
498 regulatory capacity may induce environmental baseline shifts at speeds and levels of intensity
499 outside natural boundaries and can lead to dangerous tipping points. Systemic indicators that show
500 these changes, open up opportunities for positive action on ecosystem restoration and recovery,
501 particularly in the form of new management paradigms such as ecosystem-based design approach
502 and nature-based solutions.

503 The proposed methodological way of assessing ecosystem health using thermal infrared brightness
504 temperature is potentially a useful macro-scale proxy indicator of ecosystem health due to its
505 simplicity but systemic view, and is aligned with previous studies (Gornyy et al., 2010; Wagendorp et
506 al., 2006). This systemic indicator can support a global monitoring of ecosystem wellbeing by
507 identifying critical areas that are being degraded at a fast rate (Freudenberger et al., 2013) tending
508 to states of “fever” compared with human induce changes that are regenerative and potentially
509 aligned with ecosystem-based design principles (Jørgensen, 2006b; Keesstra et al., 2017).

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Author contributions statement

DA wrote the main manuscript text, PG applied the remote sensing methodology and prepared figures 1–2, FU supported the statistical analyses and prepared figures 3–6 , PH and GPL contributed to the results analyses and discussion. All authors reviewed the manuscript.

Additional Information

Competing interests

The author(s) declare no competing interests.

Appendix

Figure 1 – Land use types used in the study based on “Carta de Ocupação do Solo da Região Autónoma da Madeira, 2007. Native ecosystems included the Laurissilva natural forest. Non-native ecosystems included Eucalyptus and Pine forest.

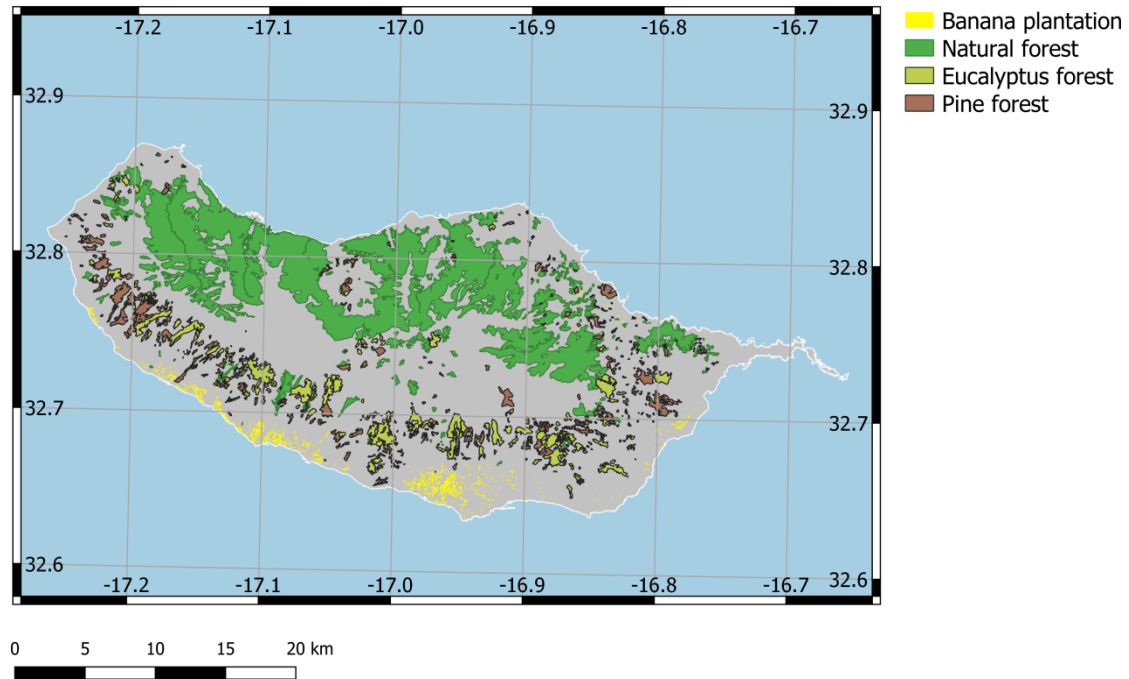


Table 1 – Classes of different attributes (altitude, slope and aspect) used in the abiotic homogenization. Class beaks follow the criteria of minimum no-correlated classes.

Altitude (meters)	< 500
	500 to 700
	700 to 1350
	> 1350
Slope (degrees)	< 12
	12 to 28
	> 28
Aspect (degrees)	< 120
	120 to 240
	> 240

Table 2 – Selected Landsat 8 images

Landsat 8 (OLI and TIRS)	Date (dd/mm/yyyy)
	19/08/2013
	10/01/2014
	11/02/2014
	27/02/2014
	02/05/2014
	21/07/2014
	06/08/2014
	22/08/2014
	07/09/2014
	09/10/2014
	19/04/2015
	05/05/2015
	08/07/2015

Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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Author contributions statement

David Avelar wrote the main manuscript text, Pedro Garrett applied the remote sensing methodology and prepared figures 1–2, Florian Ulm supported the statistical analyses and prepared figures 3–6 , Peter Hobson and Gil Penha lopes contributed to the results analyses and discussion. All authors reviewed the manuscript.

Appendix

Figure – Ecosystem types used in the study based on “Carta de Ocupação do Solo da Região Autónoma da Madeira, 2007. Native ecosystems included the Laurissilva natural forest. Non-native ecosystems included Eucalyptus and Pine forest.

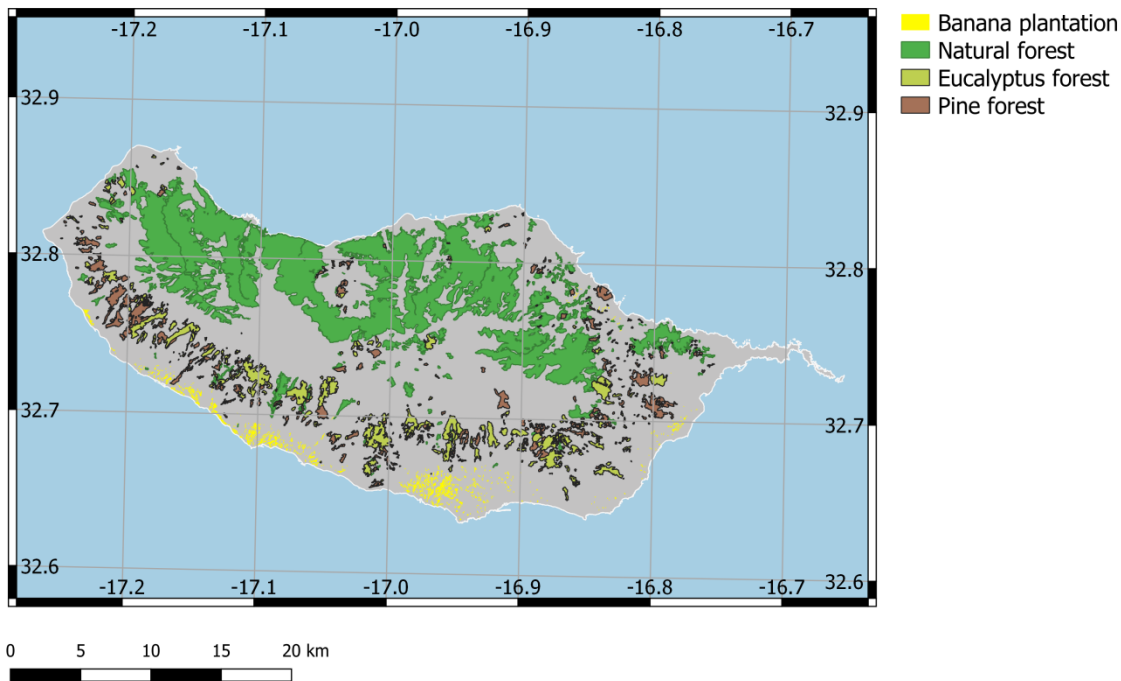


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	07/09/2014
	09/10/2014
	19/04/2015
	05/05/2015
	08/07/2015

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